Transactions of the Royal Society of S. Aust. (1994), 118(2), 133-138.

A SMALL STHENURINE KANGAROO FROM A PLEISTOCENE CAVE DEPOSIT, NULLARBOR PLAIN, WESTERN AUSTRALIA

by G. J. PRIDEAUX*

Summary

PRIDEAUX, G. J. (1994) A small sthenurine kangaroo from a Pleistocene cave deposit, Nullarbor Plain, Western Australia. *Trans. R. Soc. S. Aust.* 118(2), 133-138. 31 May, 1994.

Simosthenurus maddocki nullarborensis ssp. nov. is described from Lindsay Hall Cave, northwest of Madura Pass on the Nullarbor Plain, Western Australia. Although the upper molars are very close in morphology to *S. maddocki maddocki* Wells & Murray, 1979 from eastern Australia, they are notably smaller. The P^3 is small, narrow and inflated posteriorly. Geographic dwarfing due to resource limitations is a possible explanation for the small size of this Nullarbor subspecies.

KEY WORDS: sthenurine kangaroo, *Simosthenurus maddocki nullarborensis* ssp. nov., *Simosthenurus maddocki maddocki*, Lindsay Hall Cave, Nullarbor Plain, Pleistocene, geographic dwarfing.

Introduction

In April 1991, a recently collapsed opening to a limestone cave was discovered by members of the Western Australian Plane Caving Group on Madura Station, northwest of Madura Pass on the Nullarbor Plain (Fig. 1). Fossil material was removed from the cave, named Lindsay Hall Cave, during exploration in September 1991 and April 1992. Several cranial fragments belonging to a medium to large size sthenurine, and a very small partial left maxilla were recovered. This latter specimen represents a new form smaller than any sthenurine previously described from the Pleistocene. It most closely resembles *Simosthenurus maddocki* Wells & Murray, 1979 from eastern Australia with which it is compared. This paper describes the new sthenurine.

* School of Biological Sciences, Flinders University of South Australia, GPO Box 2100, Adelaide, S. Aust. 5001

Fig. 1. Deposits yielding *Simosthenurus maddocki* in southeastern Australia.

Material and Methods

The material is housed in the Western Australian Museum, Perth (WAM). Mensuration, dental terminology and nomenclature follow Tedford (1966). As the homology of premolar cusps is currently being re-examined by Prof. David Ride (pers. comm.), they are referred to here an anterior labial cusp, posterior lingual cusp, etc. All measurements are in millimetres. Abbreviations: L = length; AW = anterior width protoloph(id); PW = posterior width metaloph, hypolophid; AH = anterior crown height, labial side; PH = posterior height; n = sample size. Note crown height measurements are heavily dependent on degree of enamel wear.

Systematics

Order: DIPROTODONTIA Owen, 1866
Suborder: PHALANGERIDA Aplin & Archer, 1987
Superfamily: MACROPODOIDEA Gray, 1821
Family: MACROPODIDAE Gray, 1821
Subfamily: STHENURINAE (Glauert, 1926)
Genus: SIMOSTHENURUS Tedford, 1966

Simosthenurus maddocki maddocki
Wells & Murray, 1979
FIGS 1, 5

Holotype: SAM P16999, a near complete juvenile skull collected from Victoria Fossil Cave, Naracoorte, South Australia. Diagnosis, description and comparison of nominotypic form of *S. maddocki* is provided by Wells & Murray (1979). This subspecies is also recognised from Greenwater Hole Cave, near Tantanoola in South Australia (Pledge 1980), Bingara, Wombeyan Caves and Mt Fairy in New South Wales (Flannery & Hope 1983), and Lancefield in Victoria (pers. observation). Age of type locality is late Pleistocene (Wells *et al.* 1984).

Simosthenurus maddocki nullarborensis ssp. nov.
FIGS 1-5

Holotype: WAM 92.9.8, a partial left juvenile maxilla collected from Lindsay Hall Cave, near Madura, Nullarbor Plain, Western Australia (31°35′S, 126°40′E). Collected in September 1991 by Wendy Binks and Katherine Crisp, Western Australian Plane Caving Group. Age of type locality is ?late Pleistocene.

Diagnosis: Maxilla smaller than *Simosthenurus maddocki maddocki* Wells & Murray, 1979 and *Sthenurus gilli* Merrilees, 1965; molars low crowned, very similar in morphology to *S. m. maddocki*, but smaller. Molars possess very fine enamel crenulations with lophs notably convex anteriorly. P^3 very small, narrow to tapered anteriorly, but inflated posteriorly.

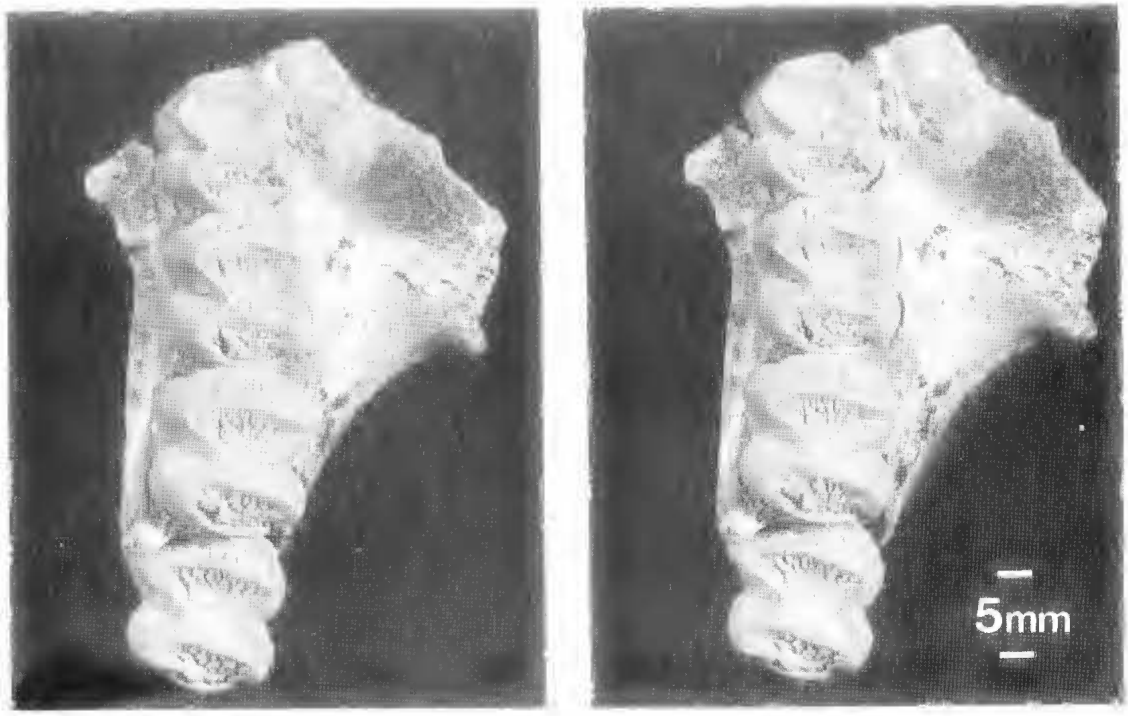

Fig. 2. Stereopair of *Simosthenurus maddocki nullarborensis* ssp. nov. left maxilla (WAM 92.9.8, holotype) in occlusal view.

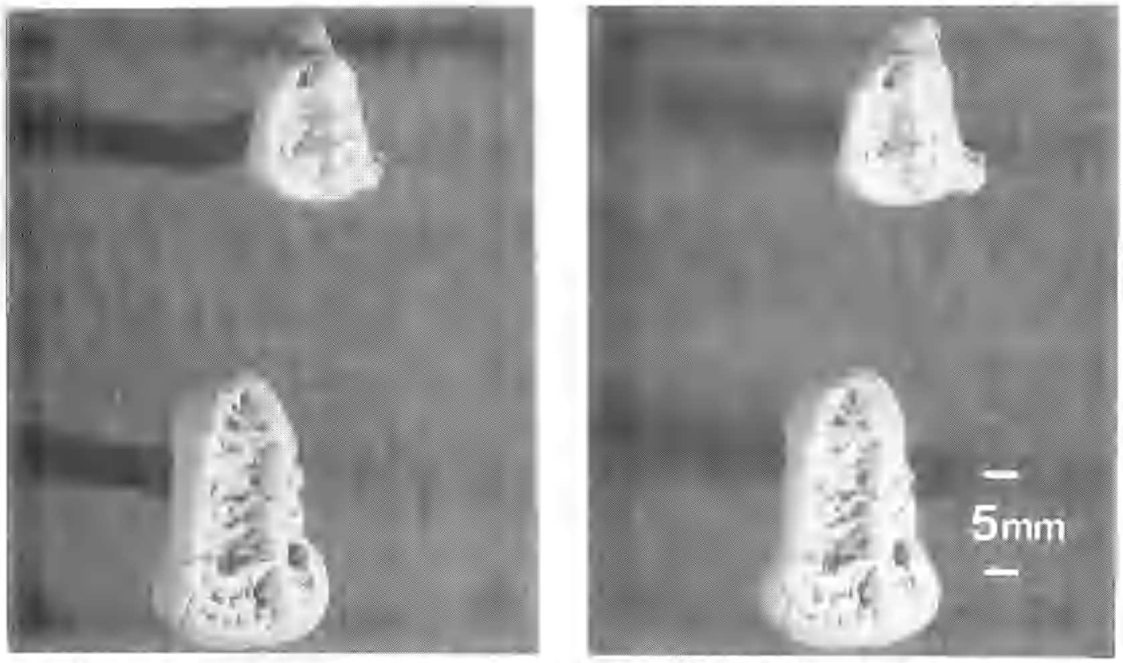

Fig. 3. Stereopairs of *Simosthenurus maddocki nullarborensis* ssp. nov. left P^2, top, and P^3, bottom, (WAM 92.9.8, holotype) in occlusal view.

Description of holotype: Maxilla (Fig. 2). Fragmentary nature of specimen has resulted in preservation of very few non-dental characters suitable for description or comparison. Palatine vacuities appear to have extended anteriorly to level of dP^3 anterior loph. Only base of masseteric process preserved in holotype making an estimation of size difficult. Posterior aspect of buccinator muscle scar is laterally wide.

Dentition (Figs 2-5, Table 1). Includes P^2, dP^3, M^{1-3}, excavated P^3, with teeth exhibiting only beginning wear.

P^2: Very small with relatively high labial crest containing prominent anterior labial cusp and small cuspules posteriorly. Transverse ridge joining labial and lingual posterior cusps encloses posterior basin. Fine transverse ridgelets occupy longitudinal basin, with anteriormost slightly larger and dividing off small anterior basin.

dP^3: Completely molariform, wider across posterior loph than anterior loph, and smaller than succeeding molars.

P^3: Posterior third of P^3 inflated both labially and lingually. Posterolabial stylar cusp is well developed but does not attain height of posterior labial cusp. Labial crest divided into three cuspules bordered at both extremes by prominent anterior and posterior cusps. Transverse ridge leading halfway into longitudinal basin from labial crest slightly overlaps with small ridge descending across from lingual crest

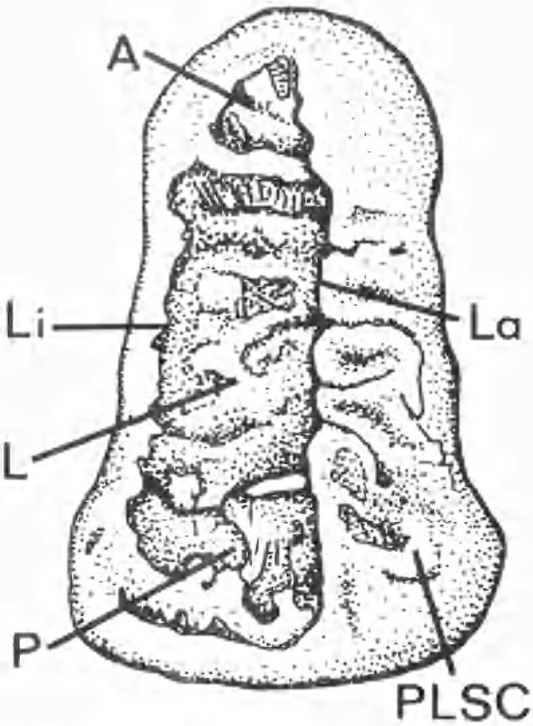

Fig. 4. Drawing of the holotype P^3 of *Simosthenurus maddocki nullarborensis* ssp. nov. A, anterior basin; P, posterior basin; L, longitudinal basin; La, labial crest; Li, lingual crest; PLSC, posterolabial stylar cusp. (Length = 13.3mm).

to form anterior border of posterior basin. Small anterior basin separated by transverse ridge descending lingually from prominent anterolabial cusp to lingual counterpart. Ridge appears to have formed from unification of two smaller ridges descending transversely from each anterior cusp.

M^{1-3}: Molars increase in length and width from M^1 to M^3 (M^4 not preserved). Respective widths across protoloph and metaloph in M^1 are identical. In M^2, protoloph wider than metaloph, and in M^3 wider again. Molars low crowned with lophs notably convex anteriorly. Very fine crenulations on molars are extensive, slightly coarser on posterior side of metaloph. Anterior cingulum well developed, but not especially broad. It extends anteriorly from tip of paracone, then labially across almost entire width of protoloph. Low, weak postprotocrista extends posterolabially from protocone and meets with very small crest originating from metaloph, forming a crista obliqua. Lingual to this structure, a deep fossette is present in median valley. Labially, a notch is formed between well developed postpara- and premetacristae. Posterior cingulum broad and formed by fine posthypocrista descending posterolabially, then labially across back of molar, and overlapping with less prominent postmetacrista.

Paratype: WAM 92.12.7, a singular, unassociated P^3 from Lindsay Hall Cave. Collected in April 1992 by Lindsay Hatcher, Western Australian Plane Caving Group.

Variation: It is only possible to get an impression of variation within *S. m. nullarborensis* by comparing the P^3 of WAM 92.9.8 and WAM 92.12.7. They differ slightly in size, namely length and posterior width, but more noticeably in morphology. Whereas the posterior third of the P^3 in WAM 92.9.8 is inflated both labially and lingually, there is only a lingual inflation in WAM 92.12.7 (Fig. 4). This is due largely to the reduced development of the posterolabial stylar cusp in WAM 92.12.7 compared to the holotype. This is an especially variable character in other sthenurines, including *S. m. maddocki* and *S. occidentalis*, and probably also represents intrasubspecific variation in *S. m. nullarborensis*. Other notable differences between the premolars are the lateral tapering present in WAM 92.9.8, where the tooth becomes more narrow anteriorly than WAM 92.12.7, and the incipient development of the anterior cingulum in WAM 92.12.7 compared to WAM 92.9.8. Intraspecific variation in premolar morphology is common in all sthenurine species for which numerous individuals are known (pers. observation).

Comparison with other taxa: Clearly, the skull of *S. m. nullarborensis* was very small even considering

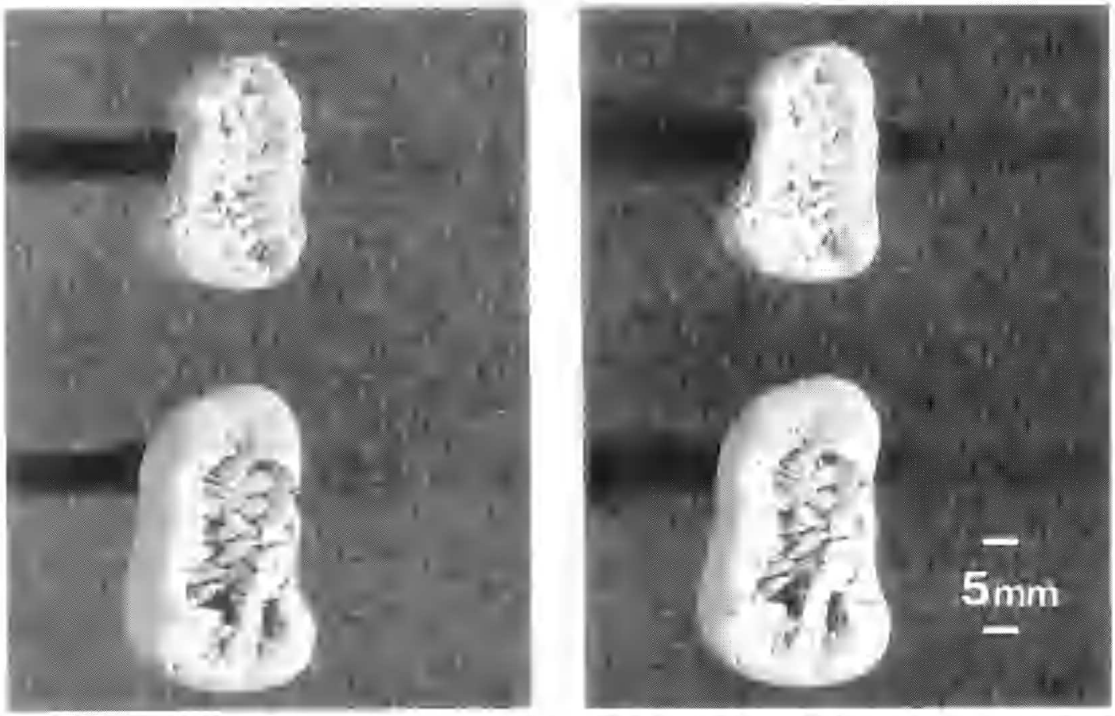

Fig. 5. Stereopair of *Simosthenurus maddocki nullarborensis* ssp. nov. P^3, top (WAM 92.12.7, paratype), and typical *Simosthenurus maddocki maddocki* P^3, bottom (SAM P27752), in occlusal view.

the difficulty involved with interpreting skull size from fragmentary juvenile specimens. The preserved maxillary region is smaller in every respect than similarly-aged individuals of *S. gilli*, previously recognised as the most diminutive extinct sthenurine. It is much smaller than similarly-aged *S. m. maddocki*. Anterior extension of the palatine vacuities and the morphology of the buccinator muscle scar in *S. m. nullarborensis* are both similar to *S. m. maddocki*.

The P^2 and P^3 of *S. m. nullarborensis* are considerably smaller than *S. m. maddocki* (Table 1). Although only two P^3 specimens were available to conduct one-tailed t-tests, both length ($t=3.3$, $P=0.09$) and anterior width ($t=30$, $P=0.01$) for *S. m. nullarborensis* fell significantly outside of the known range of *S. m. maddocki*. As with the maxilla, they are smaller in size than those of any sthenurine. Based on the comparison of mean length and width measurements, they are 24% smaller than *S. m. maddocki*.

S. m. nullarborensis and *S. m. maddocki* differ in several morphological features of the P^3. The posterolabial stylar cusp is less prominent in *S. m. nullarborensis*, especially in WAM 92.12.7. Neither specimen possesses a stylar cusp which attains the height of the posterior labial cusp, contrasting *S. m maddocki* in which the height of the stylar cusp consistently exceeds that of the posterior labial cusp. In *S. m. maddocki* the labial crest is divided into either two or three cuspules between the larger anterior and posterior labial cusps. Both *S. m. nullarborensis* specimens possess three cuspules but a similar variation in number could also occur in this subspecies. In the holotype P^3 the anterior basin is well formed and separated from the longitudinal basin by a transverse ridge (Fig. 4). This structure is not present

TABLE 1. *Cheek teeth dimensions of* Sinosthenurus maddocki nullarborensis *ssp. nov.*, S. m. maddocki *and* S. gilli *[mean (standard deviation) [observed range]]*

Tooth	Species	L	AW	PW	AH	PH	n
P^2	*S. m. nullarborensis*	7.0	4.9	5.7	5.5	5.5	1
	S. m. maddocki	9.2 (0.15) [9.0-9.4]	6.2 (0.53) [5.8-7.1]	7.3 (0.51) [6.7-8.1]	6.3 (0.49) [5.7-6.9]	6.2 (0.59) [5.7-6.9]	5
	S. gilli	10.0 (0.31) [9.6-10.5]	7.4 (0.21) [6.9-7.5]	8.9 (0.17) [8.6-9.1]	6.5 (0.23) [6.4-6.9]	6.7 (0.36) [6.3-7.3]	7
dP^3	*S. m. nullarborensis*	8.5	7.5	8.2	4.9	4.9	1
	S. m. maddocki	9.8 (0.11) [9.6-9.6]	8.7 (0.24) [8.4-9.0]	9.0 (0.36) [8.6-9.6]	5.0 (0.31) [4.6-5.5]	4.9 (0.24) [4.6-5.2]	7
	S. gilli	9.2 (0.21) [9.0-9.6]	9.2 (0.26) [8.9-9.6]	9.6 (0.32) [9.2-10.2]	4.9 (0.35) [4.3-5.3]	5.2 (0.23) [4.9-5.5]	11
P^3	*S. m. nullarborensis*	12.5 (1.13) [11.7-13.3]	5.8 (0.14) [5.7-5.9]	8.0 (0.71) [7.5-8.5]	6.5 (0.71) [6.0-7.0]	5.9 (0.21) [5.7-6.0]	2
	S. m. maddocki	16.0 (0.59) [15.3-17.0]	8.1 (0.50) [7.5-9.0]	10.1 (0.56) [9.3-11.1]	8.3 (0.30) [7.7-8.6]	7.7 (0.52) [7.1-8.6]	8
	S. gilli	16.1 (0.63) [15.2-17.1]	9.2 (0.54) [8.0-9.8]	11.4 (0.72) [10.2-12.8]	9.8 (0.98) [8.0-10.8]	9.8 (0.88) [8.3-10.8]	11
	S. andersoni	15.5 (0.53) [14.8-16.5]	7.7 (0.38) [7.2-8.2]	9.5 (0.38) [9.0-10.3]	9.4 (0.46) [8.9-10.0]	9.4 (0.68) [8.3-10.5]	8
M^1	*S. m. nullarborensis*	9.4	8.7	8.7	4.8	4.9	1
	S. m. maddocki	10.8 (0.29) [10.3-11.2]	10.1 (0.24) [9.7-10.5]	10.0 (0.44) [9.4-10.9]	5.3 (0.57) [4.8-5.7]	5.2 (0.49) [4.4-6.0]	9
	S. gilli	10.3 (0.50) [9.3-11.0]	10.2 (0.34) [9.6-10.7]	10.0 (0.33) [9.4-10.5]	5.5 (0.59) [4.3-6.2]	5.9 (0.54) [4.8-6.6]	11
M^2	*S. m. nullarborensis*	10.1	9.2	8.9	5.5	6.0	1
	S. m. maddocki	11.2 (0.21) [10.9-11.5]	10.8 (0.38) [10.5-11.6]	10.3 (0.34) [9.9-10.7]	5.5 (0.45) [4.9-6.2]	5.5 (0.47) [4.9-6.4]	7
	S. gilli	11.0 (0.49) [10.3-11.9]	10.5 (0.44) [9.9-11.0]	10.2 (0.36) [9.6-10.8]	6.1 (0.39) [5.6-6.7]	6.6 (0.33) [6.2-7.0]	11
M^3	*S. m. nullarborensis*	10.2	9.6	8.8	4.7	4.5	1
	S. m. maddocki	11.4 (0.29) [11.0-11.7]	11.1 (0.45) [10.5-11.9]	10.1 (0.48) [9.5-10.7]	5.7 (0.37) [5.0-6.2]	5.5 (0.38) [5.0-6.0]	7
	S. gilli	11.6 (0.46) [10.8-12.2]	10.7 (0.48) [10.0-11.6]	10.3 (0.50) [9.6-11.2]	6.2 (0.66) [5.5-7.8]	6.5 (0.68) [5.5-7.9]	11

in *S. m. maddocki* where inward curving of the anterior extremes of the labial and lingual crests occurs (Fig. 5). These often do not meet and result in an anterior basin which is very poorly designated or completely absent. A more intermediate condition is observed in WAM 92.12.7.

Complete molarisation of the dP^3 is characteristic of all sthenurines. Likewise, the increase in molar length and relative changes in widths along the tooth row in *S. m. nullarborensis* are typical of most species. Molar morphology is very similar to *S. m. maddocki*, making them readily separable from the similarly-sized *S. gilli*, which possesses a larger crista obliqua and less extensive fine enamel crenulations. Therefore, upper molars of the subspecies are separable on size only, with measurements of the *S. m. nullarborensis* molars approximately 13% smaller than mean values for *S. m. maddocki*.

Discussion

Although some doubt existed initially over which taxonomic rank should apply to the Nullarbor form, morphological similarity to nominotypic *S. maddocki* precluded a specific separation. Designation of fossil subspecies has previously been made in reference to dwarfing macropod lineages (Marshall & Corruccini 1978; Dawson & Flannery 1985). They are an effective form of recognising clear-cut temporal or geographical variants within a species. Size reduction in P^3 and molar dimensions (24% and 13% respectively) from *S. m. maddocki* to *S. m. nullarborensis* is comparable to that observed by Marshall & Corruccini for other medium to large-sized macropods from the Pleistocene to Holocene. They concluded that resource limitations probably accounted for dwarfing in these macropods and *Sarcophilus harrisii*. Dwarfing is commonly observed in island populations contemporaneous with large mammal populations on the mainland (Lomolino 1985). A similar effect between mainland regions caused by climatic unpredictability, which today typifies the Nullarbor Plain, may also have been significant in the Pleistocene environment, perhaps leading to size reduction in *S. m. nullarborensis*.

Interestingly, analysis of size variation in *Thylacinus cynocephalus* from the Nullarbor Plain (Lowry 1972) did not statistically separate (as a subspecies) the population sample from larger *T. cynocephalus*, even though several small individuals were present. Unfortunately, the lack of *S. m. nullarborensis* material at this stage prevents a more thorough statistical analysis than that conducted for the permanent premolar. However, dimensions of most measurements fall well outside the known range of *S. m. maddocki* supporting its current designation as a separate subspecies.

A probably late Pleistocene age is attributed to the Lindsay Hall Cave deposit, based on the similarity of *S. m. nullarborensis* to *S. m. maddocki*, and the co-occurrence of another widespread, but undescribed sthenurine. The bone-bearing strata of Lindsay Hall Cave may equate with unit 2 in Madura Cave (Lundelius 1963; Lundelius & Turnbull 1989) which has also yielded this undescribed species. Support for this would rely on a detailed stratigraphic investigation of cave deposits in the area.

Acknowledgments

Thanks to Dr Rod Wells (Flinders University), Dr John Long (W.A. Museum) and an anonymous reviewer for offering comments on the manuscript. Dr Long also provided Fig. 4, and with Dr Alex Baynes, was responsible for loan of the fossil material. I am grateful to the Western Australian Plane Caving Group for their efforts, particularly Wendy Binks, Katherine Crisp and Lindsay Hatcher who discovered the deposit and collected fossil material from the site.

References

Dawson, L. & Flannery, T. F. (1985) Taxonomic and phylogenetic status of living and fossil kangaroos and wallabies of the genus *Macropus* Shaw (Macropodidae: Marsupialia) with a new subgeneric name for the large wallabies. *Aust. J. Zool.* **33**, 473-498.

Flannery, T. F. & Hope, J. H. (1983) Occurrences of the extinct macropodid marsupial *Simosthenurus maddocki* in New South Wales. *Aust. Mammal.* **6**, 37-39.

Lomolino, M. V. (1985) Body size of mammals on islands: the Island Rule re-examined. *Amer. Nat.* **125**, 310-316.

Lowry, J. W. J. (1972) The taxonomic status of small fossil thylacines (Marsupialia, Thylacinidae) from Western Australia. *J. R. Soc. W. Aust.* **55**, 19-29.

Lundelius, E. L., Jr. (1963) Vertebrate remains from the Nullarbor Caves, Western Australia. *Ibid.* **46**, 75-80.

_____ & Turnbull, W. D. (1989) The mammalian fauna of Madura Cave, Western Australia Part VII: Macropodidae: Sthenurinae, Macropodinae, with a review of the marsupial portion of the fauna. *Fieldiana, Geol.* **17**(rts), 1-71.

Marshall, L. G. & Corruccini, R. S. (1978) Variability, evolutionary rates, and allometry in dwarfing lineages. *Paleobiology* **4**, 101-119.

Pledge, N. S. (1980) Macropodid skeletons, including: *Simosthenurus* Tedford, from an unusual "drowned cave" deposit in the southeast of South Australia. *Rec. S. Aust. Mus.* **18**, 131-141.

Tedford, R. H. (1966) A review of the macropodid genus *Sthenurus*. *Univ. Calif. Publ. Geol. Sci.* **57**, 1-72.

Wells, R. T. & Murray, P. F. (1979) A new sthenurine kangaroo (Marsupialia, Macropodidae) from southeastern South Australia. *Trans. R. Soc. S. Aust.* **103**, 213-219.

_____ Moriarty, K. & Williams, D. L. G. (1984) The fossil vertebrate deposits of Victoria Fossil Cave Naracoorte: an introduction to the geology and fauna. *Aust. Zool.* **21**, 305-333.